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REVISION OF THE WIND RIVER FAUNAS, EARLY EOCENE OF CENTRAL WYOMING. PART 10. *BUNOPHORUS* (MAMMALIA, ARTIODACTYLA)

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Abstract

Bunophorus is a senior synonym of *Wasatchia* and includes six species that occur in the early and middle Eocene of North America: *B. etsagicus* (type species), *B. grangeri* (=*W. lysitensis* and *W. dorseyana*), *B. pattersoni, B. macropternus, B. sinclairi* (=*B. gazini*) and *B. robustus* (=*Diacodexis robustus*). *B. sinclairi* includes two penecontemporaneous geographic variants: *B. s. sinclairi* from the Wind River, Piceance and Green River basins, and *B. s. robinsoni,* n. ssp., from the Huerfano Basin. Cladistic analysis of the dental evidence implies that *B. robustus* is the most primitive species, with *B. grangeri, B. pattersoni* and a clade comprising *B. etsagicus, B. macropternus* and *B. sinclairi* progressively more derived. The polarities of shared-derived dental features and the implied relationships among these taxa are consistent with the stratigraphic record. The pattern of evolution in *Bunophorus,* as revealed by the dentition, appears to be strictly cladogenetic, without any of the significant anagenetic change observed in its sister taxon, *Diacodexis,* over the same period of time. Sister species of *Bunophorus* are distinguished by marked dental changes and each species has a relatively short geologic range. *B. macropternus* is restricted to the Lysitean; its widespread occurrence makes it an excellent biostratigraphic indicator of that subage. Similarly, the co-occurrence of *B. etsagicus, B. grangeri* and *B. pattersoni* implies a Lysitean age, whereas *B. sinclairi* first appears in the Lostcabinian and continues into the Gardnerbuttean.

Introduction

Bunophorine artiodactyls have been known since 1875 when Cope described "*Antiacodon crassus*" from the early Eocene of New Mexico. Two years later, Cope (1877) transferred this species to the genus, *Sarcolemur,* but the holotype of *S. crassus* was subsequently lost and mention of the species by the turn of century became limited to taxonomic compendia (Trouessart, 1898; Hay, 1902). As a result, we (Krishtalka and Stucky, 1986) declared *S. crassus* to be a *nomen oblitum.* From Cope's (1877) figure of *S. crassus,* it is evident that the holotype bore the diagnostic characters of *Wasatchia* and *Bunophorus,* genera named and described by Sinclair in 1914 and included with *Diacodexis, Homacodon, Helohyus, Microsus* and others in the Dichobunidae. Gazin (1955) essentially followed this scheme but united *Wasatchia, Bunophorus* and *Diacodexis* in a new subfamily "Diacodexinae." Guthrie (1968) thought that *Wasatchia* and *Diacodexis* were congeneric, retaining *Bunophorus* as a separate genus. Van Valen (1971) retained *Diacodexis* and correctly recognized that *Wasatchia* and *Bunophorus* were too similar morphologically to warrant generic separation, a conclusion

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provisionally supported elsewhere (Krishtalka and Stucky, 1986) and corroborated here.

Eight species of *Wasatchia* and *Bunophorus* have been named. Sinclair (1914) originally included species in *Bunophorus* previously assigned to *Mioclaenus, Pantolestes* and *Trigonolestes* (*B. etsagicus*) and *Phenacodus* (*B. macropternus*); these were known only from the Bighorn Basin. His three species of *Wasatchia*—*W. grangeri, W. dorseyana, W. lysitensis*—were also based on material from the Willwood Formation, Bighorn Basin. The paratype of *W. lysitensis* (AMNH 14936) was from the Lysite Member of the Wind River Formation and one specimen of *W. dorseyana* (AMNH 16295) was from the San Juan Basin.

Almost 40 years later, the Wind River Basin yielded records of *B. etsagicus* (White, 1952), *B. macropternus* and *Wasatchia* sp. cf. *W. dorseyana* (Kelley and Wood, 1954), but all three specimens of the latter were later reidentified as *Didymictis* (Guthrie, 1967).

In 1966, Guthrie named *B. sinclairi* based on White's (1952) *B. etsagicus* material from the Boysen Reservoir area and the type specimen from the Lost Cabin Member near Arminto (CM loc. 34). He also referred to this species one specimen allegedly from the Lysite Member (Guthrie, 1967). The "Lysite" specimen is actually also from CM loc. 34 in the Lost Cabin Member.

In 1968, Guthrie described the hindlimb structure of *Bunophorus.* Later, in his review of the Lost Cabin Member fauna, Guthrie (1971) synonymized *B. sinclairi* with *B. etsagicus* and named a new species, *B. gazini* from the type locality of *B. sinclairi,* CM loc. 34. Most recently, we (Krishtalka and Stucky, 1986) described a new species, *Wasatchia pattersoni,* from the early Eocene of the Piceance and Huerfano basins, and transferred *Diacodexis robustus* to *Wasatchia.*

Study of available material has resulted in the following systematic conclusions. (1) *Bunophorus* is a senior synonym of *Wasatchia* and includes six valid species: *B. etsagicus* (type species), *B. grangeri* (=*W. lysitensis* and *W. dorseyana*), *B. pattersoni, B. macropternus, B. sinclairi* (=*B. gazini*) and *B. robustus* (=*Diacodexis robustus*). (2) *B. sinclairi* includes two penecontemporaneous geographic variants: *B. s. sinclairi* from the Wind River, Piceance and Green River basins, and *B. s. robinsoni,* n. ssp., from the Huerfano Basin.

Abbreviations are as follows: ACM, Amherst College Museum, Amherst; AMNH, American Museum of Natural History, New York; CM, The Carnegie Museum of Natural History, Pittsburgh; FMNH-P, Field Museum of Natural History, Paleontology, Chicago; JHU, Johns Hopkins University, Baltimore (R. Bakker collection); PU, Princeton University, Princeton; UCM, University of Colorado Museum, Boulder; UM, University of Michigan, Ann Arbor; USNM, National Museum of Natural History, Washington; UW, University of Wyoming, Laramie; YPM, Yale Peabody Museum, New Haven; L, length; W, width. All measurements are in millimeters.

SYSTEMATICS

Family Diacodexeidae (Gazin, 1955)
Subfamily **Bunophorinae,** new subfamily

Diagnosis.—P3/3–M3/3 more robust than in Diacodexeinae, with proportionately more inflated P4/4 and molar cusps and conules, P_4 paraconid more reduced, P^4 lacking metacone, M^{1-2} more nearly square and conular wings reduced or absent; included species larger than all Diacodexeinae except *Simpsonodus* sp. (Krishtalka and Stucky, 1986) and *Diacodexis secans* (only some specimens in lineage segment *D. s.-secans*; Krishtalka and Stucky, 1985).

Included genera.—*Bunophorus* Sinclair, 1914 (=*Wasatchia* Sinclair, 1914).

Known distribution.—Early to middle Eocene (Wasatchian to early Bridgerian), North America; early Eocene (Ypresian), Europe.

Bunophorus Sinclair, 1914

Wasatchia Sinclair, 1914:268
Bunophorus Sinclair, 1914:273

Diagnosis.—As for Subfamily Bunophorinae.

Type species.—*Bunophorus etsagicus* (Cope, 1882).

Included species.—Type species and *B. robustus* (=*Diacodexis robustus* Sinclair, 1914), *B. grangeri* (=*Wasatchia grangeri* Sinclair, 1914, including *W. dorseyana* Sinclair, 1914 and *W. lysitensis* Sinclair, 1914), *B. pattersoni* (=*W. pattersoni* Krishtalka and Stucky, 1986), *B. macropternus* (Cope, 1882), *B. sinclairi* Guthrie, 1966 (including *B. gazini* Guthrie, 1971), ?*B. cappettai* Sudre *et al.,* 1983.

Known distribution.—Early to middle Eocene (Wasatchian to early Bridgerian), North America; early Eocene (Ypresian), Europe.

Discussion.—Sinclair (1914) distinguished *Bunophorus* from *Wasatchia* on the basis of a lack of diastemata between the lower premolars, more robust lower premolars, vestigial or absent molar paraconids, a narrower M_3 talonid relative to the trigonid, and a more strongly convex mandible ventrally—features that appeared to be diagnostic given the seven specimens available to Sinclair. Much larger collections now indicate that these characters are variable within species previously assigned to both genera and are not diagnostic at the generic level. For example, the molar paraconid is vestigial on most specimens of *B. macropternus* and *B. sinclairi,* but is as well developed on individual molars of some specimens as the molar paraconid in "*Wasatchia*" *grangeri.*

Gazin (1952) and Van Valen (1971) reached conclusions similar to ours, but Gazin retained the status quo whereas Van Valen synonymized *Wasatchia* and *Bunophorus* under the latter. Robinson (1966) also opted to retain the two genera on the basis of different wear patterns, but this feature too is highly variable. Finally, Guthrie (1968) synonymized *Wasatchia* with *Diacodexis*—an action rejected by Van Valen (1971) and subsequent workers (Schankler, 1980; Krishtalka and Stucky, 1985).

Study of the holotypes and large collections of the species of *Wasatchia* and *Bunophorus* indicates that, as Van Valen (1971) concluded, generic separation is unwarranted. Although *Wasatchia* has page priority in Sinclair (1914), *Bunophorus* has priority according to Article 24 (action of the first reviewer; Van Valen, 1971) of the International Code of Zoological Nomenclature (1985). Named species of the two genera do not differ morphologically from one another to any greater degree than do species of *Diacodexis* (Krishtalka and Stucky, 1985). Moreover, as the cladogram of relationships indicates (Fig. 8), retention of *Wasatchia* and *Bunophorus* for their respective species would make the latter paraphyletic.

Bunophorus etsagicus (Cope, 1882)
(Fig. 1; Table 1)

Mioclaenus etsagicus Cope, 1882:189
Pantolestes etsagicus (Cope, 1882), Cope 1883:547; 1884:717, 724, plate 25e, fig. 24; 1886:618; Trouessart, 1898:800.

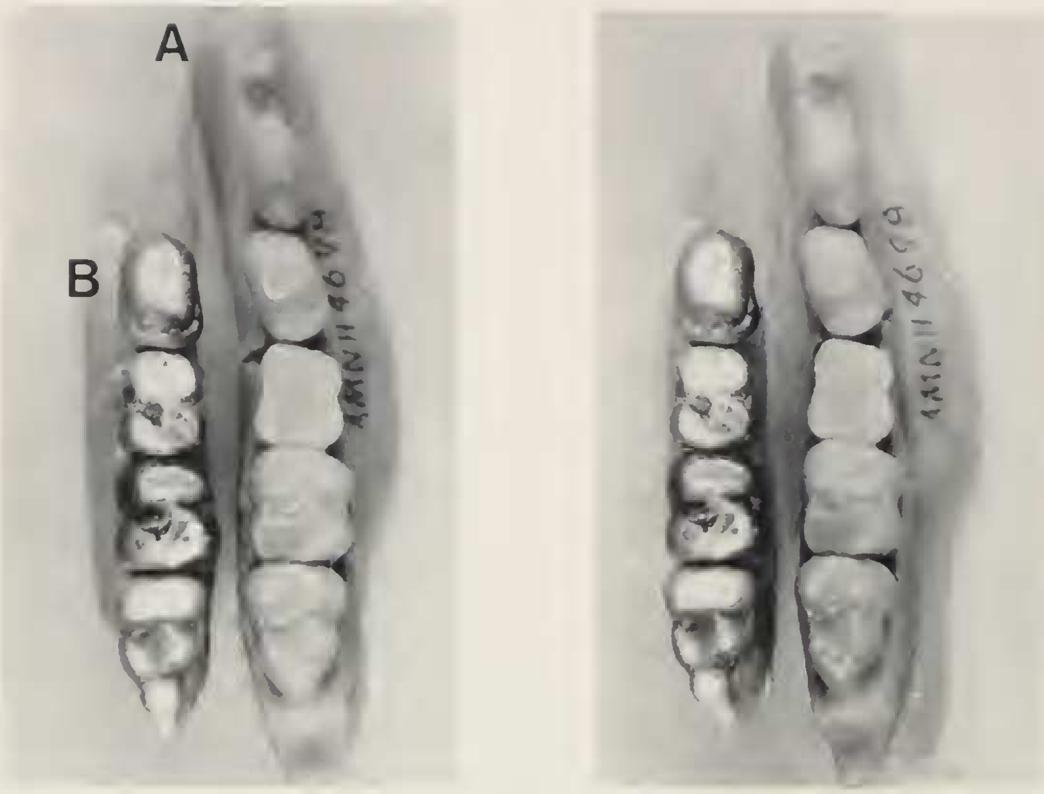


Fig. 1.—*Bunophorus etsagicus.* (A) AMNH 4698, right dentary of holotype; (B) CM 37322. Approx. ×1.6.

Trigonolestes etsagicus (Cope 1882), Matthew, 1899:34.
Bunophorus etsagicus (Cope, 1882), Sinclair, 1914:273, fig. 7; Guthrie, 1967:47.

Holotype.—AMNH 4698, LP_3–M_3, RP_3–M_3, from the Willwood Formation, Bighorn Basin, Wyoming.

Diagnosis.—Differs from *B. robustus, B. grangeri* and *B. pattersoni* in having a vestigial to absent M_{1-3} paraconid, and in lacking a paraconid on P_4; unlike *B. macropternus,* P_4 not as hyperinflated in proportion to M_1, and M_3 without labial cingulid; unlike *B. sinclairi* and *B. pattersoni,* P_4 more inflated (and anteriorly bulbous) in proportion to M_1; unlike *B. sinclairi,* P_4 lacking metaconid, M_{1-3} with stronger, uninterrupted cristid obliqua, and P_4–M_3 less bunodont, with trigonid higher than talonid; larger than *B. robustus, B. macropternus* and *B. pattersoni.*

Referred specimens.—CM 20874, 37322, ACM 2757, USNM 187494.

Localities.—CM locs. 810, 927, ACM loc. 60-118 (all Lysitean, Lysite Mbr., Wind River Fm.); USNM loc. TR-50-B (Lysitean, Indian Meadows Fm.), all Wind River Basin, Wyoming.

Known distribution.—Middle Wasatchian (Lysitean)—Wind River Basin (Wind River Fm., Indian Meadows Fm.), Wyoming; Wasatchian (holotype, subage indeterminate)—Bighorn Basin (Willwood Fm.), Wyoming.

Discussion.—*B. etsagicus* is known from only five specimens of the lower dentition from the Bighorn (holotype) and Wind River basins. The exact provenance and age of the holotype is unknown. In the Wind River Basin, *B. etsagicus* is restricted to the Lysitean, during which time it co-occurs with *B. macropternus, B. grangeri,* the diacodexeine *Diacodexis secans* (lineage segment *D. s.-kelleyi*) and the homacodontid *Hexacodus pelodes.*

Bunophorus etsagicus shares the derived feature of a weak or vestigial molar

Table 1.—*Dimensions of lower dentition of* Bunophorus etsagicus. *Abbreviation: BHB, Bighorn Basin.*

		P_3		P_4		M_1		M_2		M_3	
Specimen	Loc.	L	W	L	W	L	W	L	W	L	W
AMNH 4698	BHB	7.4	3.8	7.5	4.8	7.1	6.0	7.7	7.2	9.1	6.7
AMNH 4698	BHB	7.4	3.9	—	—	—	—	7.6	7.2	9.1	6.7
CM 37322	927	7.7	4.4	7.9	5.4	7.1	5.9	7.5	7.0	9.0	6.5
USNM 187494	TR50B			7.4	4.7	—	—	—	—	—	—
CM 20874	810					7.2	6.6	—	—	—	—
ACM 2757	60-118					7.1	6.9	—	—	—	—

paraconid with *B. macropternus, B. pattersoni* and *B. sinclairi* (Fig. 8) and may be most closely related to the former given their common possession of an inflated, anteriorly bulbous P_4 in relation to M_1.

Bunophorus macropternus (Cope, 1882)
(Fig. 2; Table 2, 3)

Phenacodus macropternus Cope, 1882:179–180; 1884:433, 490, plate 25e, fig. 15; Matthew, 1899:32; Trouessart, 1898:725.
Bunophorus macropternus (Cope, 1882), Sinclair, 1914:275, fig. 8; Kelley and Wood, 1954:364, fig. 15b, c; Guthrie, 1967:47, fig. 33.
Bunophorus, cf. *macropternus* (Cope, 1882), Gazin, 1952:72; 1962:82, plate 14, figs. 6, 8.

Holotype.—AMNH 4395, RM_{1-2}, from the Willwood Fm., Bighorn Basin, Wyoming.

Diagnosis.—Distinguished from all species of *Bunophorus* by hyperinflation of P4/4 (in proportion to M1/1) and lingual area of M^{1-3}; strong cingulid on M_3. Additionally: unlike *B. robustus, B. grangeri* and *B. pattersoni* (most), P_4 paraconid absent, M_{1-3} paraconid vestigial or absent; differs from *B. sinclairi* in lacking a metaconid on P_4 and pericone, hypocone and isolated metaconule on M^{1-2}, and retaining a complete, distinct cristid obliqua on M_{1-3}.

Referred specimens.—In addition to material referred elsewhere (Gazin, 1952:72, 1962:82), CM 19909, 20874, 21893, 22798–22800, 37110, 39681, 39984, 42098–42100, 43141, 43738, 62607, 62612, 62613; USNM 19209; ACM 2415, 2756, 2779, 2816, 10196, 11103, 11110, 11194, 11204.

Localities.—CM locs. 35, 36, 112, 113, 118, 130, 211, 803, 806, 807, 808, 928, 932, 1009, 1091; ACM locs. 48-96, 51-L13, 51-L24, 51-L25, 60-112, 60-118, 62-17—all Lysitean, Lysite Mbr., Wind River Fm., Wind River Basin, Wyoming. USNM loc. "east side of Green River," Green River Basin (Lysitean, Wasatch Fm.), Wyoming.

Known distribution.—Middle Wasatchian (Lysitean)—Wind River Basin (Wind River Fm.), Bighorn Basin (Willwood Fm.), Green River Basin (Wasatch Fm.), Wyoming.

Discussion.—*Bunophorus macropternus,* well-represented from Lysitean horizons in Wyoming, has a diagnostic dentition. P4/4 is hyperinflated in proportion to M1/1 and the lingual region of M^{1-3} is hyperinflated in proportion to crown size. Upper molars lack a definite hypocone, pericone and medial conulecristae, and the metaconule is not isolated from the protocone. P_3 is as long as or longer than P_4, but the latter is more robust and dominated by an inflated protoconid. The paraconid, weak on M_{1-3}, is reduced to a shelf-like cingulid on P_4, where a weak paracristid may also occur. M_3 bears a cingulid below the hypoconid.

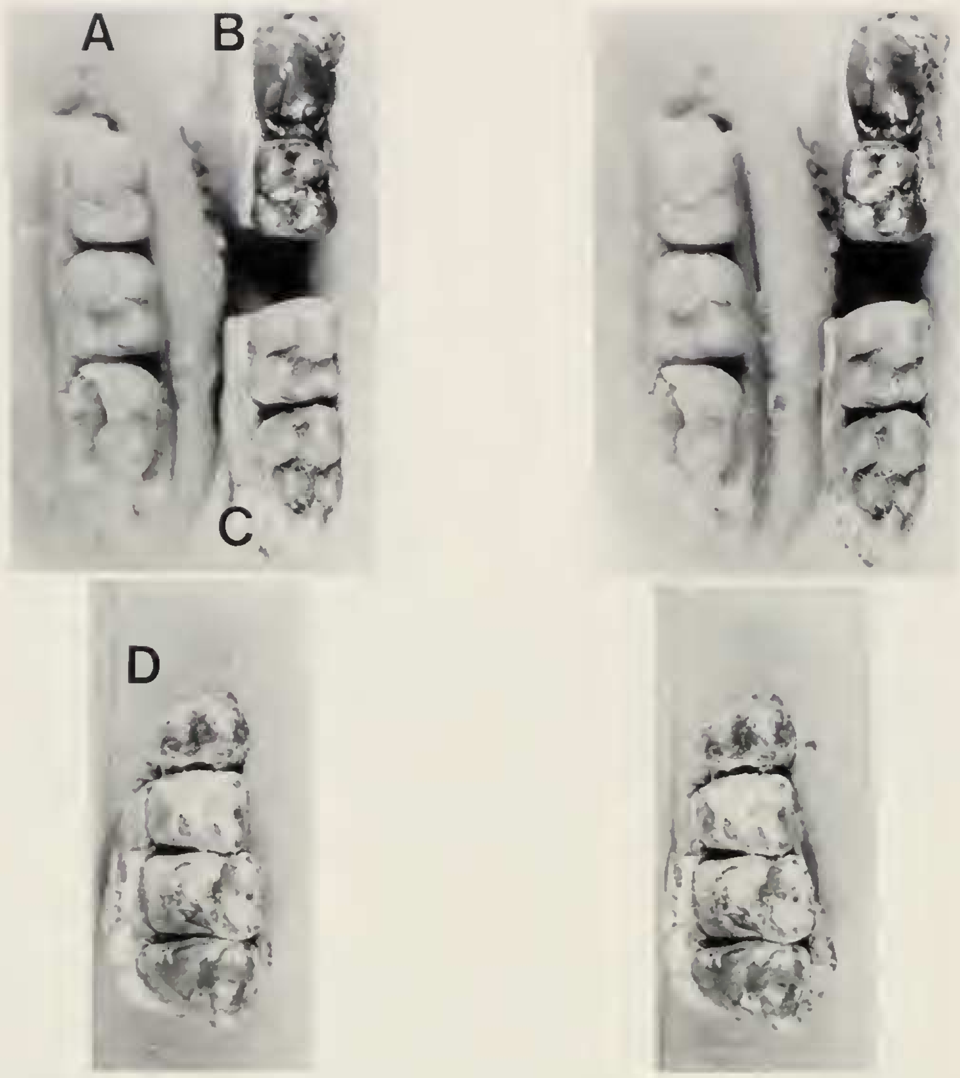


Fig. 2.—*Bunophorus macropternus.* (A) AMNH 4395, holotype; (B) USNM 19209; (C) CM 22798; (D) CM 39681. All approx. ×1.5.

Bunophorus macropternus may be most closely related to *B. etsagicus,* based on the common possession of a more inflated and anteriorly bulbous P_4 in proportion to M_1. *B. macropternus* is smaller, however, and is more derived in having hyperinflated P4/4 and lingual area of M^{1-3}. The two species co-occur in the Lysite Member of the Wind River Formation with the artiodactyls *B. grangeri, Diacodexis secans* (lineage segment *D. s.-kelleyi*) and *Hexacodus pelodes.*

None of the material that Kihm (1984) or Robinson (1966) allied with *B. macropternus* belongs here. These specimens, from the Piceance and Huerfano basins, are referred below and elsewhere (Krishtalka and Stucky, 1986) to *B. grangeri, B. pattersoni* and *B. sinclairi.*

Bunophorus sinclairi Guthrie, 1966

Bunophorus etsagicus (Cope, 1882), White, 1952:201, fig. 79; Guthrie, 1971:89, fig. 22a.
Bunophorus, cf. *etsagicus* Gazin, 1962:82, pl. 14, figs. 7, 9.
Bunophorus sp. cf. *B. macropternus* (Cope, 1882), Robinson, 1966:69, pl. 10, figs. 8, 10, in part; Kihm, 1984:285, in part.
Bunophorus sinclairi Guthrie, 1966:487, fig. 1; Guthrie, 1967:48, fig. 34; Stucky, 1982:219, fig. 49; Krishtalka and Stucky, 1986, fig. 6.
Bunophorus gazini Guthrie, 1971:90, fig. 22b.
Phenacodus vortmani Cope, 1880; West, 1973:137, in part.

Table 2.—*Dimensions of lower dentition of* Bunophorus macropternus. *Abbreviations: BHB, Bighorn Basin; GRB, Green River Basin.*

Specimen	Loc.	P_3 L	P_3 W	P_4 L	P_4 W	M_1 L	M_1 W	M_2 L	M_2 W	M_3 L	M_3 W
CM 39984	928	—	—	7.2	4.8	6.3	5.1				
CM 43738	928	6.6	3.4	6.6	4.3						
CM 19909	1091	7.1	3.8	7.0	4.7						
CM 62613	112			7.2	4.6						
USNM 19209	GRB			7.6	7.6	6.3	5.5				
CM 42098	1009					6.1	5.3				
ACM 11103	51-L13					—	—	6.5	6.0	8.5	6.2
ACM 2816	Lysite Mbr.					6.3	5.3	6.2	6.0	—	—
ACM 11110	51-L13					6.2	5.2				
AMNH 4395	BHB					6.4	5.1	7.1	6.1		
CM 22798	211							6.6	6.1	8.6	5.7
CM 22800	808							7.1	6.3		
CM 22799	113							—	—	8.1	5.7
ACM 11204	51-L25							7.1	6.3		
ACM 2756	60-112							6.5	6.0		
CM 21893	928									8.7	5.8
CM 37110	928									8.0	5.8

Holotype.—PU 13448, RP_4M_{2-3}, LP_4–M_2, from CM loc. 34 [=Sullivan Ranch; Guthrie's (1971) loc. 1; AMNH loc. Davis Ranch; PU loc. 5 mi. NW of Arminto] Lost Cabin Mbr., Wind River Fm., Wind River Basin, Wyoming.

Diagnosis.—Differs from all other species of *Bunophorus* in having (1) an incipient to definite metconid on P_4, (2) a pericone (often), large hypocone and isolated metaconule on M^{1-2}, (3) a weak, incomplete cristid obliqua on M_{2-3}, and (4) an expanded, bulbous entoconid and low, bulbous, subequal molar trigonid and talonid on M_{1-3}. Also, P4/4 more gracile (less inflated, less bulbous anteriorly) than in *B. etsagicus* and relatively much more gracile than in *B. macropternus*; M_{1-3} paraconid vestigial to absent, unlike *B. robustus, B. grangeri, B. pattersoni*; P_4 lacks paraconid, unlike *B. robustus* and some *B. grangeri*; larger than *B. robustus, B. macropternus, B. pattersoni.*

Included subspecies.—Bunophorus sinclairi sinclairi, B. s. robinsoni.

Known distribution.—Late Wasatchian to early Bridgerian (Lostcabinian to Gardnerbuttean)—Wind River Basin (Wind River Fm.), Wyoming, Huerfano

Table 3.—*Dimensions of upper dentition of* Bunophorus macropternus.

Specimen	Loc.	P^4 L	P^4 W	M^1 L	M^1 W	M^2 L	M^2 W	M^3 L	M^3 W
CM 39681	803	4.6	7.0	5.9	7.1	6.5	8.1	6.3	8.2
CM 62607	130	6.1	7.7						
ACM 11194	51-L24					6.5	8.6		
ACM 10196	48-96					6.4	8.5		
CM 42100	1091							6.0	8.6
CM 42099	1091							6.0	8.1
ACM 2415	62-17							6.3	8.4
ACM 2779	60-118							6.0	8.2

Basin (Huerfano Fm.), Colorado; late Wasatchian (Lostcabinian)—Piceance Basin (Debeque Fm.), Colorado, Green River Basin (Wasatch Fm.), Wyoming.

Discussion.—We here resurrect *B. sinclairi*, a species that Guthrie (1967, 1971) named and then synonymized with *B. etsagicus*. *Bunophorus sinclairi* is more derived than *B. etsagicus* in having a metaconid (incipient or prominent) on P_4, a weak, interrupted cristid obliqua on M_{1-3} and molar talonids and trigonids that are lower, more bulbous and subequal in height. Conversely, *B. etsagicus* is differently derived in having a robust, anteriorly inflated P_4 in proportion to M_1, a trait shared with *B. macropternus*. Also, Guthrie's (1971) holotype (and only specimen) of *B. gazini* is not, as he thought, distinguished by large size, but lies within the upper range of variation of *B. sinclairi* and is conspecific with the latter.

Importantly, Guthrie (1967) erred when he reported ACM 10093, M_{1-2} of *B. sinclairi*, from the Lysite Member of the Wind River Formation. The specimen is actually from the type locality of the species (CM loc. 34, Gardnerbuttean, Lost Cabin Mbr.). As such, *B. sinclairi* is restricted to the Lostcabinian and Gardnerbuttean and, among species of *Bunophorus*, is penecontemporaneous with *B. pattersoni* in the Huerfano Basin.

Study of the entire sample of *B. sinclairi* reveals a substantial amount of morphological variation, affecting the strength of the metaconid on P_4, the paraconid on M_{1-3}, the mesostyle on M^3 and the hypoconulid on M_3. The P_4 metaconid (n = 12) is incipient on CM 22500, weak but more distinct on UCM 42188 and CM 55099, and well developed on remaining specimens. Some P_4s (CM 22500; PU 13488, holotype; UCM 16475) bear accessory talonid cusps, as do many M_2s and M_3s either in the center of the talonid basin (for example, CM 37259) or between the hypoconid and hypoconulid (for example, PU 13488). The molar paraconid, if present, is most evident on M_1 as a small bulge on the anterior face of the metaconid, and is barely discernable on M_{2-3}. Many of the M^3s bear a week mesostylar flexure, which is best developed on CM 46931. The variation described here applies not only to the entire sample of *B. sinclairi*, but to individual samples from each locality.

In addition, there appear to be two major patterns of clinal variation: stratigraphic and geographic. Wind River Lostcabinian material is, on average, slightly larger than Wind River Gardnerbuttean material—a pattern also evident in *Diacodexis secans*, lineage segment *D. s.-secans* (Krishtalka and Stucky, 1985). Concerning the pattern of geographic variation, Gardnerbuttean material from the Wind River Basin is, on average, slightly smaller than penecontemporaneous material from the Huerfano Basin. Also, M_{2-3}s from Huerfano have a more nearly complete cristid obliqua, whereas those from the Wind River bear a weaker cristid obliqua that rarely reaches the base of the trigonid (being interrupted by a deep notch) and is often indicated only by a wear facet. This geographic variation is expressed taxonomically by subspecific distinction of the Huerfano Basin material as *B. s. robinsoni*, n. ssp., an action in keeping with the philosophy expressed elsewhere (Krishtalka and Stucky, 1985): in paleontology, as in neontology, subspecies should be reserved for reflecting geographic patterns of morphological variation among penecontemporaneous populations of a species.

Bunophorus sinclairi sinclairi
(Fig. 3; Table 4, 5)

Holotype.—PU 13488, holotype of *B. sinclairi*.

Diagnosis.—Gardnerbuttean individuals slightly smaller than penecontempora-

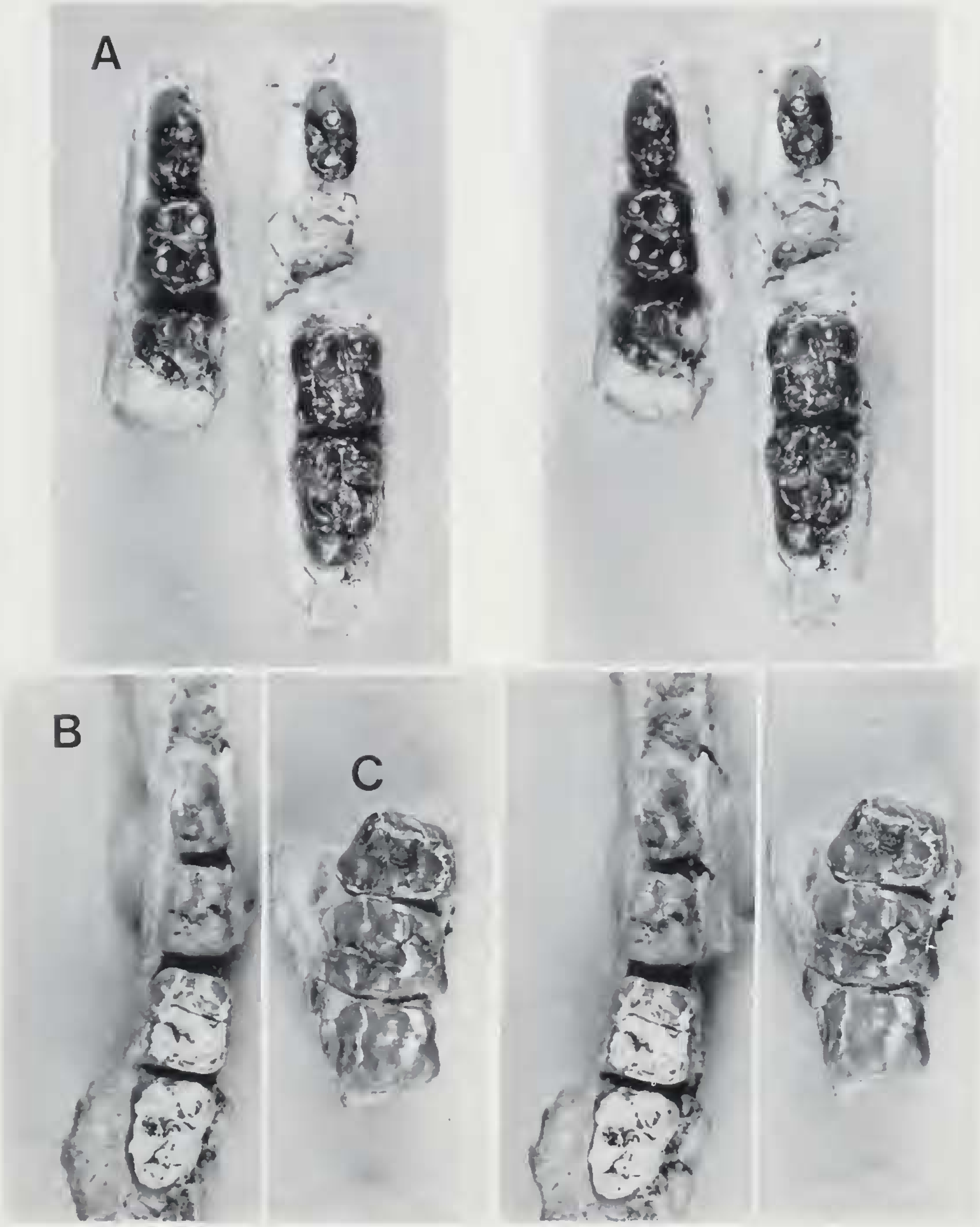


Fig. 3.—*Bunophorus sinclairi.* (A) PU 13448, holotype, *B. s. sinclairi*; (B) YPM 16475, holotype, *B. s. robinsoni*; (C) AMNH 17485, *B. s. robinsoni.* All approximately ×1.4.

neous *B. s. robinsoni*; M_{2-3} cristid obliqua weaker, interrupted by notch at base of trigonid.

Referred specimens.—CM 21112, 21123, 21124, 21127, 21205, 21206, 21938, 21939, 21951, 22359, 22483 (holotype of *B. gazini*), 22486–22489, 22491–22501, 22525, 26504–26508, 29136, 36431–36436, 36940, 37244–37249, 37251, 37252, 42066–42070, 42075, 42077, 42078, 42081, 42083–42086, 42088, 42089, 42093, 42094, 42116, 42117, 42132, 43142, 43480–43487, 43489, 43719, 43720, 43728, 43729, 43739–43741, 43743, 44847, 44848, 55099, 55100, 55218, 55518–55521, 62614–62617; FMNH-P 15509, 26792; AMNH 14940; ACM 10093; UW 12389; PU 13452; USNM 18370, 22244, 22245; UCM 42188, 43018, 44409, 45308, 46806, 46807, 46981, 47025.

Localities.—Lostcabinian: CM locs. 90, 91, 105, 858, 1039, 1040, 1041, 1042,

Table 4.—*Dimensions of lower dentition of* Bunophorus sinclairi sinclairi *and* Bunophorus sinclairi robinsoni.

Specimen	Loc.	P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W
B. s. sinclairi											
CM 55521	34	7.1	4.2								
CM 55099	34	7.3	4.2								
CM 22500A	34	7.4	3.4	7.5	4.2	7.7	6.4	8.0	7.4		
CM 42067	34			7.5	5.0						
CM 42093	1046			7.7	4.2	7.4	6.6	8.1	7.3	10.2	6.5
CM 22494	1039			8.0	5.0	7.2	6.7				
CM 21938	34			8.0	4.5						
CM 36431	34			8.3	4.7	7.5	6.4	—	—	10.2	6.7
CM 22488	34			7.0	4.2	6.8	5.9				
PU 13448	34			7.5	4.2	7.3	6.5	—	—		
PU 13448	34			7.6	4.3			8.0	6.8	10.0	6.9
CM 42078	1036					5.9	4.8	6.7	5.5		
CM 42084	1040					7.3	6.4				
CM 29136	34					6.5	5.7				
CM 22496	1039					7.2	6.4				
CM 26507	34					7.5	6.8			—	—
CM 36435	34					7.1	6.7				
CM 55519	34					7.7	7.0				
CM 37245	34					8.0	6.6				
CM 55520	34					7.6	6.7				
CM 37249	34					7.6	6.9				
CM 22483	34					8.1	6.8	9.0	8.4		
CM 21205	34					6.7	5.9	7.3	6.8		
CM 21206	34					7.3	6.6	7.8	7.1	9.5	7.0
CM 42083	1039					7.5	6.7	8.0	7.6	9.8	7.7
CM 22501	34					6.7	5.8	6.9	6.5	8.0	6.6
CM 22489	34					7.4	6.8	7.9	—		
CM 37251	34					7.6	6.5	7.8	6.8	9.4	6.6
CM 42066	34							7.8	7.0		
CM 42070	34							7.3	6.8		
CM 42085	1040							7.5	—		
CM 42077	1036							7.7	6.8		
CM 22491	91							7.3	6.7	10.1	7.3
CM 22492	91							7.5	7.4	9.4	6.7
CM 22495	1039							7.8	7.1		
CM 22493	1039							7.2	6.8		
CM 22498	1039							7.5	6.7		
CM 21112	34							8.0	—		
CM 21123	34							7.5	6.8	9.0	6.9
CM 21951	34							7.5	6.5		
CM 26508	34							8.0	7.4		
CM 36436	34							7.5	6.7		
CM 42117	34							8.1	7.4		
CM 42116	34							8.8	8.0	10.6	8.3
CM 37252	34							8.5	7.7	9.5	7.2
CM 22486	34							7.6	7.0	—	—
CM 22500B	34							8.2	6.9		
CM 22487A	34							—	—	8.4	7.1
CM 42068	34									9.1	6.7
CM 42094	1078									8.8	6.4
CM 22525	34									9.4	6.7
CM 22497	1039									9.4	7.0
CM 22499	90									9.3	6.8

Table 4.—*Continued.*

Specimen	Loc.	P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W
CM 21124	34									9.0	6.7
CM 21939	34									9.5	6.7
CM 26505	34									9.9	7.0
CM 55100	34									9.2	6.7
CM 22487B	34									8.9	6.8
CM 44847	34					—	—	7.9	7.1		
CM 43719	34									9.4	7.3
CM 43480	1077									10.2	7.3
CM 62616	1044									9.4	6.8
CM 36940	34									9.2	9.0
B. s. robinsoni											
YPM 16475	HF II			8.0	4.7	7.3	6.1	—	6.9	10.0	7.0
AMNH 17487	HF II					6.7	5.7	7.5	6.7	9.6	6.5
UCM 36447	HF II					7.3	5.9	—	—		
UCM 32745	HF II					7.1	5.9				
AMNH 17561	HF IV							6.7	5.8	8.1	5.4
UCM 42727	HF VI							8.2	6.5		
UCM 33274	HF II									9.8	6.7

1044, 1046, 1059, 1077, 1541 (Lost Cabin Mbr., Wind River Fm., Wind River Basin); UCM locs. 80062, 81008 (Red Creek facies, Wind River Fm., Wind River Basin); FMNH-P loc. 369-41 (Debeque Fm., Piceance Basin); FMNH-PM loc. NF-1, USNM loc. "southeast of Big Piney" (Wasatch Fm., Green River Basin). Gardnerbuttean: CM locs. 34, 1036, 1037, 1078; UCM locs. 79040, 79041, 80065, UW loc. V-78049, USNM loc. 48FR76 (Lost Cabin Mbr., Wind River Fm., Wind River Basin).

Known distribution.—Late Wasatchian to early Bridgerian (Lostcabinian to Gardnerbuttean)—Wind River Basin (Wind River Fm.), Wyoming; late Wasatchian (Lostcabinian)—Piceance Basin (Debeque Fm.), Colorado, Green River Basin (Wasatch Fm.), Wyoming.

Bunophorus sinclairi robinsoni, new subspecies.
(Fig. 3; Table 4, 5)

Etymology.—In recognition of Peter Robinson's contributions to the vertebrate paleontology of the Huerfano and Wind River basins.

Holotype.—YPM 16475, RP_4–M_3, from Huerfano loc. II, Huerfano Formation, Huerfano Basin, Colorado.

Diagnosis.—Gardnerbuttean individuals slightly larger than penecontemporaneous *B. s. sinclairi*; cristid obliqua on M_{2-3} more distinct.

Referred specimens.—AMNH 17485, 17487, 17561; UCM 32745, 33274, 36447, 42727; YPM 16472.

Localities.—Huerfano locs. IV, VI (Lostcabinian); Huerfano locs. II, V, "5 mi N. Gardner Butte" (Gardnerbuttean), all Huerfano Fm., Huerfano Basin, Colorado.

Known distribution.—Late Wasatchian to early Bridgerian (Lostcabinian to Gardnerbuttean)—Huerfano Basin (Huerfano Fm.), Colorado.

Table 5.—*Dimensions of upper dentition of* Bunophorus sinclairi sinclairi *and* Bunophorus sinclairi robinsoni.

Specimen	Loc.	M^1 L	M^1 W	M^2 L	M^2 W	M^3 L	M^3 W
B. s. sinclairi							
CM 26504	34	6.9	8.4	7.2	9.3	6.8	8.6
CM 42075	34	6.8	7.9			7.7	10.5
CM 36432	91	7.1	8.5				
CM 42069	34			7.5	9.9	6.0	8.5
CM 55518	34			7.1	9.2	6.5	8.5
CM 26506	34			7.0	9.0	6.8	8.6
CM 37248	34			7.1	8.7		
CM 37247	34			—	10.0		
CM 36433	91			7.4	10.5		
CM 42086	1040					7.3	9.4
CM 42089	1041					7.5	9.4
CM 42081	1039					8.0	10.4
CM 37244	34					7.5	9.6
CM 37246	34					7.2	10.0
CM 42132	105					7.1	9.4
CM 43484	1040					6.6	9.7
B. s. robinsoni							
AMNH 17485	HF II	7.6	8.5	8.1	9.8	7.8	9.8
YPM 16472	HF II	7.3	7.9	7.9	9.2	7.4	8.8

Bunophorus grangeri (Sinclair, 1914)
(Fig. 4; Table 6, 7)

Antiacodon crassus Cope, 1875:17
Sarcolemur crassus Cope, 1877:149, plate 45, fig. 16, *nomen oblitum.*
Wasatchia grangeri Sinclair, 1914:269, fig. 1; Krishtalka and Stucky, 1986, fig. 4.
Wasatchia dorseyana Sinclair, 1914:269, fig. 2–4.
Wasatchia lysitensis Sinclair, 1914:271, fig. 5–6.
Bunophorus dorseyanus (Sinclair, 1914), Lucas *et al.,* 1981.
Bunophorus grangeri (Sinclair, 1914), Lucas *et al.,* 1981.
Bunophorus sp. cf. *B. macropternus* (Cope, 1882), Kihm, 1984:285, in part.

Holotype.—AMNH 15516, RP_3–M_2, LP_4–M_3, from the Willwood Fm., "2 mi. west of St. Joe," Bighorn Basin, Wyoming.

Diagnosis.—M_{1-3} paraconid unreduced, unlike all other species of *Bunophorus* (except *B. robustus*); unlike *B. robustus,* P_4 paraconid vestigial in most specimens; differs from *B. macropternus* and *B. etsagicus* in having a gracile, uninflated P_4, and from *B. macropternus* in lacking lingually hyperinflated P^4–M^3 and a cingulid on M_3; distinguished from *B. sinclairi* by lack of metaconid on P_4, no hypocone or pericone on M^{1-3}, and strong, complete cristid obliqua on M_{2-3}; larger than *B. robustus, B. pattersoni, B. macropternus.*

Referred specimens.—In addition to material referred elsewhere (Krishtalka and Stucky, 1986), CM 22819, 42114, 51973–51975, 51978–51980; AMNH 15660 (holotype of *W. lysitensis*), 15673 (holotype of *W. dorseyana*); UM 66033, 64071, 64497, 64162 (tentatively), 64121, 64136 (tentatively) 64364, 65999; UCM (JHU) unnumbered specimens.

Localities.—Graybullian: CM loc. Dorsey Creek, AMNH loc. "head of Dorsey Creek", UCM (JHU) locs. "W-NM," "TH," "3TR," "MON," "RON," "OPS" (Willwood Fm., Bighorn Basin, Wyoming); Lysitean: CM locs. 116, 1093 (Wind

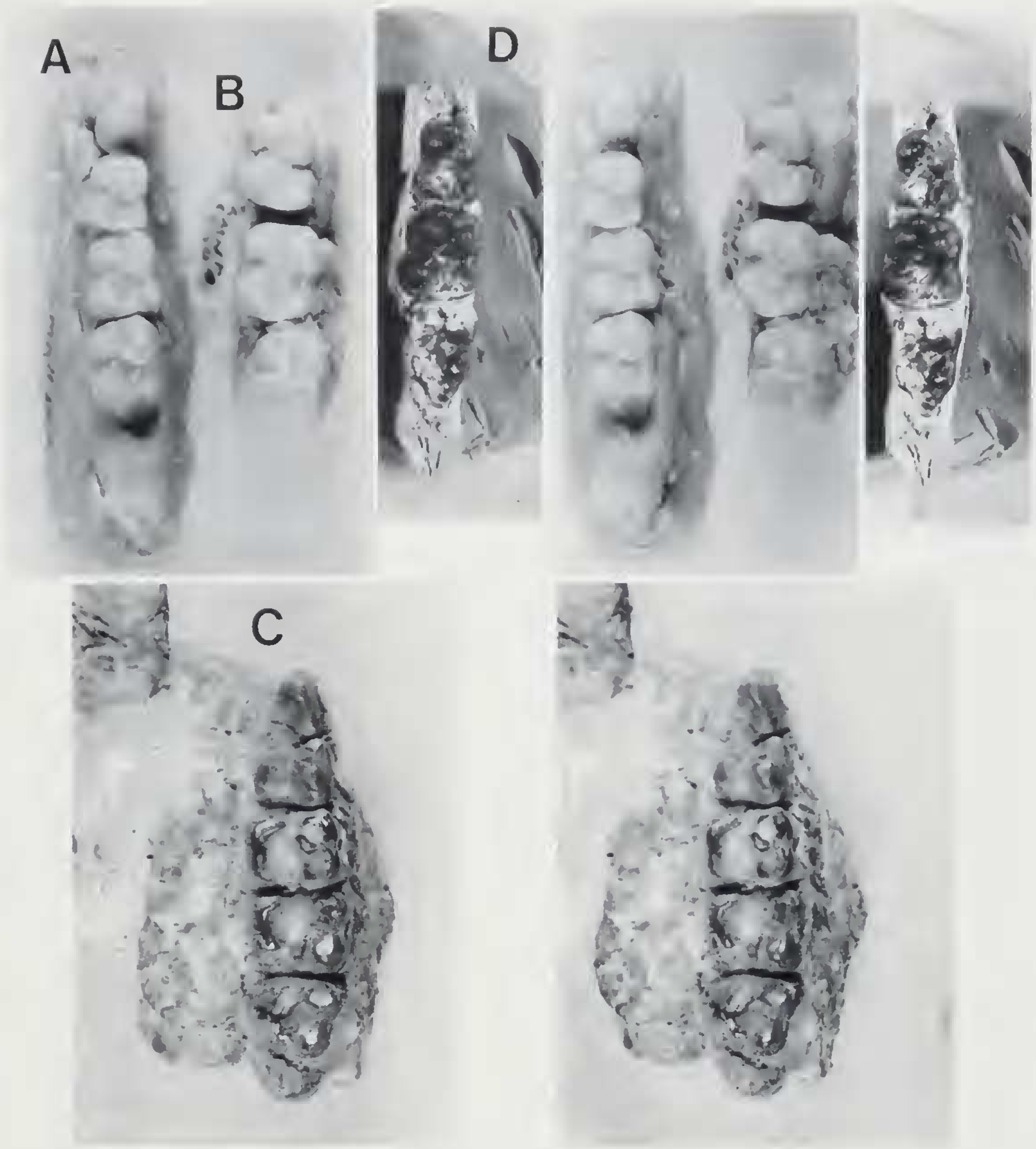


Fig. 4. *Bunophorus grangeri.* (A) AMNH 15516, holotype (part); (B) AMNH 15660 (holotype, *W. lysitensis*); (C) AMNH 15673 (holotype, *W. dorseyana*); (D) AMNH 48003. All approx. ×1.3.

River Fm., Wind River Basin), AMNH loc. 15 Mile Creek, (Willwood Fm., Buffalo Basin), UM locs. Y-RB3, Y-M421, Y-431, Y-M45 (Willwood Fm., Bighorn Basin), Wyoming.

Known distribution.—Wasatchian: late Graybullian—Piceance Basin (Debeque Fm.), Colorado; late Graybullian and/or early Lysitean—San Juan Basin (San Jose Fm.), New Mexico; Graybullian to Lysitean—Bighorn Basin (Willwood Fm.), Wyoming; Lysitean—Wind River Basin (Wind River Fm.), Wyoming.

Discussion.—*B. grangeri,* recently discussed by us as *Wasatchia grangeri* (Krishtalka and Stucky, 1986:190), is represented by substantial collections from the early Wasatchian of the Bighorn, Piceance and San Juan basins. Its first appearance in the Bighorn Basin marks the onset of Schankler's (1980) *Bunophorus* Interval Zone, and its first occurrence in other basins may be a reliable biostratigraphic indicator of the late Graybullian.

As McKenna (1960) suspected, larger collections of *Bunophorus* from the Big-

Table 6.—*Dimensions of lower dentition of* Bunophorus grangeri *and* Bunophorus robustus. *Abbreviations: BHB, Bighorn Basin; FM, Four Mile. See also Krishtalka and Stucky, 1986, for more dental measurements of* B. grangeri.

Specimen	Loc.	P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W
B. grangeri											
AMNH 15516	BHB	6.5	3.5			6.8	5.6	7.5	6.8		
AMNH 15516	BHB			7.0	4.1	6.7	5.6	7.5	6.8	9.3	6.1
UM 66033	Y-RB3			7.8	4.6	8.1	6.4	8.3	7.2	9.4	6.7
UCM no num	BHB-W-NM			7.2	4.0			7.2	6.4	8.7	6.2
UCM no num	BHB-3TR			6.9	3.9						
AMNH 15660	BHB					—	—	8.6	7.8	—	—
AMNH 15660	BHB					7.9	6.5	—	—	9.7	6.6
UM 64364	Y-M431					7.0	5.5	7.5	6.5	9.0	6.5
UM 64364	Y-M431					6.4	5.0	—	—	7.6	5.0
UM 65999	Y-M45					7.5	6.5	8.4	7.9		
UM 64497	Y-M421					7.0	6.6				
UM 64071	Y-M421					—	—	7.5	6.4		
UCM no num	BHB-TH					7.1	5.6				
UCM no num	BHB-TH					—	—	7.6	6.6	9.5	6.5
CM 22819	116							8.9	6.9		
CM 51973	1093							7.4	7.1	8.9	6.1
CM 51980	1093							7.6	6.6		
UM 64364	Y-M431							—	—	8.9	6.5
UM 64121	Y-M421							7.6	6.5	8.5	6.2
CM 42114	797									8.3	6.4
CM 51979	1093									7.9	6.0
AMNH 15673	BHB									8.9	6.2
UCM no num	BHB-MON									8.7	6.3
B. robustus											
AMNH 80506	FM	6.9	3.9								
AMNH 15512	BHB			6.2	3.9	5.5	4.6				
AMNH 92885	BHB					5.5	4.4				
AMNH 15105	BHB							6.2	5.7	—	—
AMNH 15514	BHB							6.0	4.9	7.4	4.9
AMNH 80502	FM									7.9	4.8
CM 36914	878							5.8	5.5	7.8	5.3

horn Basin (including excellent uncatalogued UCM material) indicate that *W. dorseyana* is conspecific with *B. grangeri.* Sinclair's (1914) diagnostic criteria—overall size, size of M_3 hypoconid, P_3 paraconid, M_1 cingulid development—have proven to be variable and overlapping.

Similarly, *W. lysitensis* is a junior synonym of *B. grangeri.* We erred (Krishtalka and Stucky, 1986) in tentatively referring *W. lysitensis* to *Simpsonodus.* Material from the Bighorn Basin (type locality of *W. lysitensis*) made available to us since then include P_4 and unworn M_{1-3}, unlike the holotype and described specimens of *W. lysitensis* (Guthrie, 1967; Sinclair, 1914). Study of this material indicates that *W. lysitensis* is indistinguishable from *B. grangeri.* Curiously, Sinclair (1914) differentiated *W. lysitensis* from *Helohyus,* but did not distinguish it from other species he ascribed to *Wasatchia* and *Bunophorus.*

Bunophorus grangeri is more primitive than all other species of *Bunophorus* except *B. robustus* in retaining a well-developed paraconid on M_{1-3}, but is more derived than the latter in its larger size and the proportionately reduced paraconid

Table 7.—*Dimensions of upper dentition of* Bunophorus grangeri *and* Bunophorus robustus. *Abbreviation: BHB, Bighorn Basin.*

		P^3		P^4		M^1		M^2		M^3	
Specimen	Loc.	L	W	L	W	L	W	L	W	L	W
B. grangeri											
CM 51975	1093	6.9	5.0	6.0	7.6	6.3	8.1				
AMNH 15673	BHB	—	—	6.2	7.3	6.8	7.7	7.4	8.3	6.9	8.4
AMNH 15673	BHB			—	—	6.8	7.6	7.4	8.3	6.9	8.4
CM 51978	1093			5.9	7.6						
UCM no num	BHB-3TR			5.9	7.0	—	—	—	—	7.3	8.8
UM 64136	Y-M421					6.2	7.5				
UM 64162	Y-M421					6.2	7.8	7.0	8.2		
UCM no num	BHB-TH					—	—	7.6	9.8	—	—
CM 51974	1093							—	—	6.5	8.3
UCM no num	BHB-OPS							7.4	9.6	6.3	9.2
UM 64364	Y-M431									7.3	9.0
UCM no num	BHB-RON									7.0	8.2
B. robustus											
CM 38800	953									5.0	6.7

on P_4. There is intraspecific variation in the strength of the paraconid on P_4 (weak to absent) and M_3 (weak to strong), the hypoconulid on M_3, the cingular hypocone on M^{1-2}, and degree of enamel crennulation.

Bunophorus pattersoni (Krishtalka and Stucky, 1986), new combination
(Fig. 5)

Bunophorus sp. cf. *B. macropternus* (Cope, 1882), Robinson, 1966:69, in part, pl. X, fig. 11; Kihm, 1984:285, in part.
Wasatchia pattersoni Krishtalka and Stucky, 1986:192, fig. 5.

Holotype.—FMNH-P26590, RP_4–M_3, from the Debeque Formation, Piceance Basin, Colorado.

Emended diagnosis.—Paraconid vestigial to absent on P_4, unlike *B. robustus*; M_{1-3} proportionately more inflated and paraconid weaker than in *B. robustus, B. grangeri*; M_{1-3} paraconid stronger than in *B. macropternus, B. etsagicus, B. sinclairi*; P_4 gracile, uninflated, unlike in *B. macropternus, B. etsagicus*; differs from *B. sinclairi* in having a strong cristid obliqua on M_{2-3} and lacking a metaconid on P_4; smaller than *B. grangeri, B. etsagicus* and *B. sinclairi.*

Known distribution.—Middle to late Wasatchian (Lysitean to Lostcabinian)—Piceance Basin (Debeque Fm.), Colorado; earliest Bridgerian (Gardnerbuttean)—Huerfano Basin (Farisita Fm.), Colorado.

Discussion.—This species was named and described elsewhere (Krishtalka and Stucky, 1986) as *Wasatchia* (rather than *Bunophorus*) *pattersoni,* but as noted above, *Bunophorus* has priority.

One of the specimens, FMNH-P 26807, is unusually smaller than the rest of the sample from the Piceance Basin (Krishtalka and Stucky, 1986, Table 4), and may prove to be specifically distinct. It is equal in size to the largest specimen of *Diacodexis secans,* lineage segment *D. s.-secans* (CM 21017; Krishtalka and Stucky, 1985, Fig. 2E) and is very similar to that taxon in such convergent features as reduction of molar paraconid, inflated cusps (especially the metaconid), a talonid

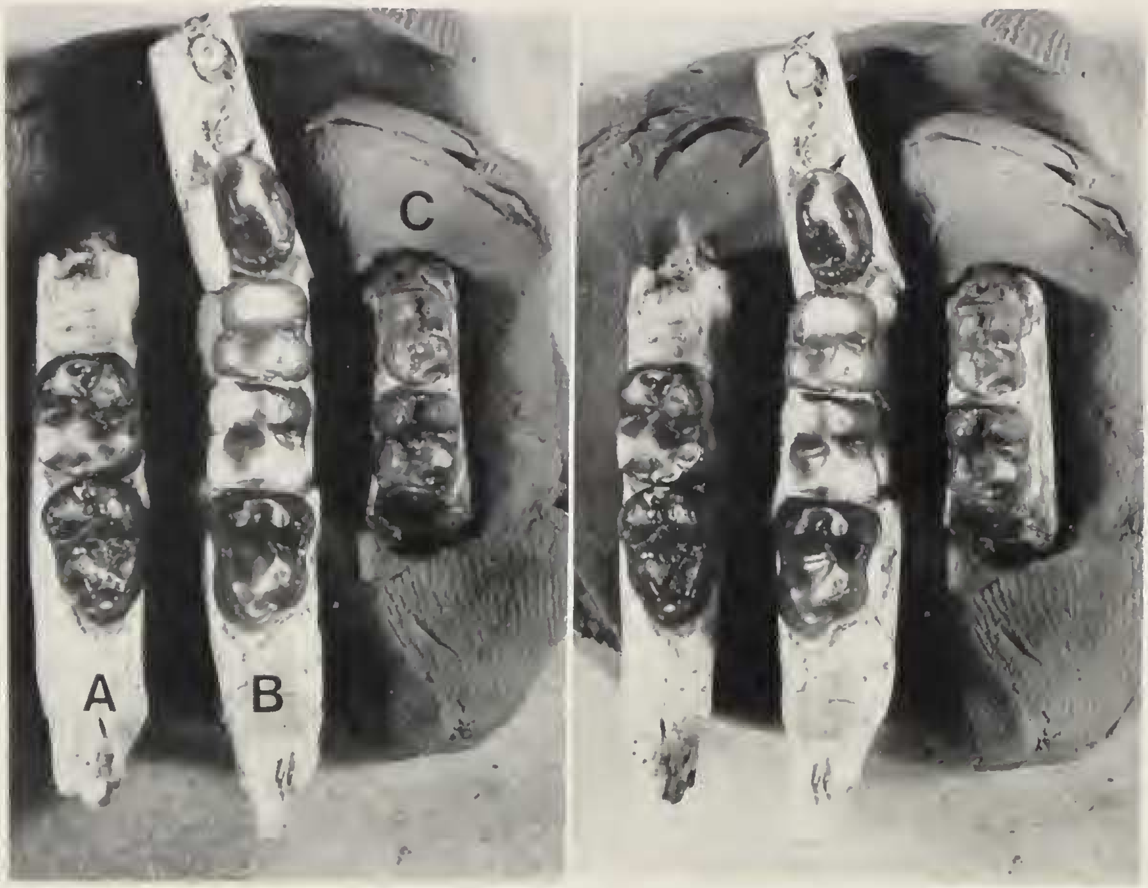


Fig. 5.—*Bunophorus pattersoni.* (A) AMNH 17561; (B) FMNH-P 26590, holotype; (C) FMNH-P 26807. All approx. ×2.

notch and squared M_2. *D. s.-secans* is distinct from *B. pattersoni* in its less bulbous molar hypoconid, deeper and wider talonid basin, and more gracile P_4 with a strong paraconid.

On two specimens of *B. pattersoni* with unworn lower molars (FMNH-P 26536, 26807) the paraconid is stronger and more cusp-like than in *B. macropternus, B. etsagicus* and *B. sinclairi,* but is significantly weaker than in *B. robustus* and *B. grangeri.* On one other unworn specimen (FMNH-P 26636), the paraconid is absent from M_3, faint and medial on M_2, and stronger on M_1. All of the other referred molars are more worn and bear weak facets in the paraconid position. Given this molar morphology and that of P_4 (vestigial paraconid, no metaconid), *B. pattersoni* appears to be more derived than *B. robustus* and *B. grangeri* but less so than other species of *Bunophorus,* for which it is also a suitable morphological ancestor.

Bunophorus robustus (Sinclair, 1914), new combination
Fig. 6; Table 6, 7)

Diacodexis robustus Sinclair, 1914:293 in part, fig. 27A, C.
Wasatchia sp. McKenna, 1960:120.

Holotype.—AMNH 15514, LM_{2-3}, from the "Lower Graybull Valley," Willwood Formation, Bighorn Basin, Wyoming.

Diagnosis.—Differs from all other species of *Bunophorus* (except *B. grangeri*) in having prominent paraconid on P_4–M_3 and less bunodont molar cusps; differs

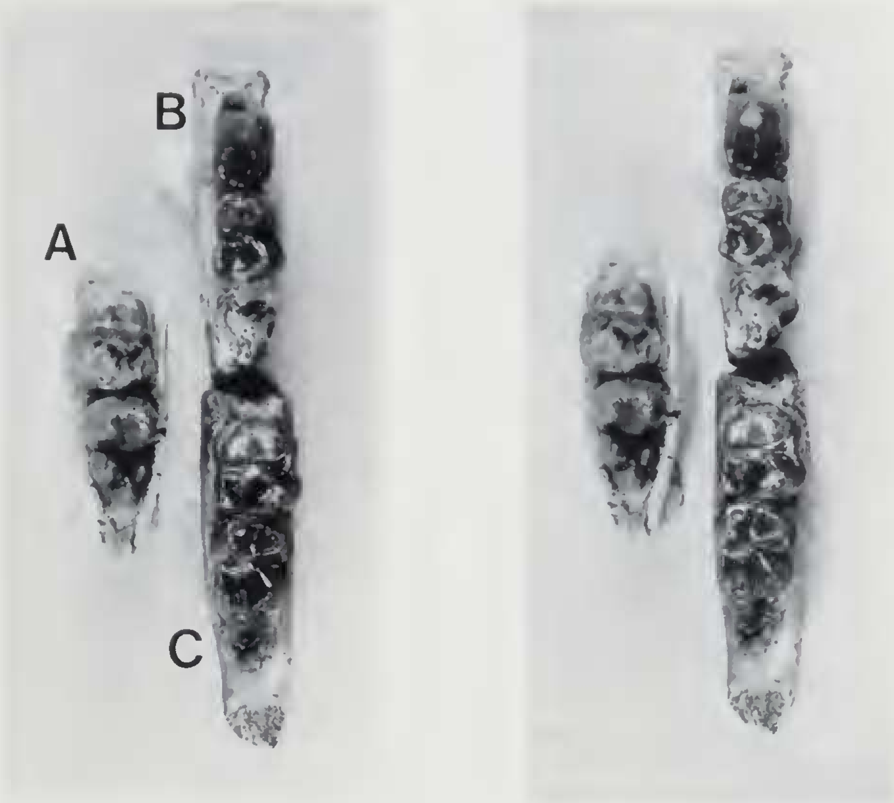


Fig. 6.—*Bunophorus robustus.* (A) AMNH 15514, holotype; (B) AMNH 15512; (C) CM 36914. All approx. ×1.7.

from *B. grangeri* in having a paraconid on P_4. Additionally: P_4 not as inflated as in *B. etsagicus, B. macropternus*; unlike *B. sinclairi,* P_4 lacks metaconid, M_{2-3} cristid obliqua strong and complete; much smaller than *B. grangeri, B. etsagicus, B. sinclairi* and slightly smaller than *B. pattersoni, B. macropternus.*

Referred specimens.—In addition to material referred elsewhere (McKenna, 1960 to "*Wasatchia* sp."), CM 36914, 38800; AMNH 15105, 15512, 80506, 92885.

Localities.—CM locs. 878, 953; AMNH locs. "lower Graybull Valley", "lower fork of Dorsey Creek" (all Graybullian, Willwood Fm., Bighorn Basin, Wyoming); UCMP locs. V-5357, V-5421 (Sandcouleean, Four Mile area, Wasatch Fm., Colorado).

Known distribution.—Early Wasatchian: Graybullian—Bighorn Basin (Willwood Fm.), Wyoming; Sandcouleean—Sand Wash Basin (Wasatch Fm.), Colorado.

Discussion.—Compared to species of *Diacodexis,* the known dentition of *B. robustus* (P_4–M_3, M^3) is, as its name suggests, more robust, P_4 is more inflated and the paraconid on P_4 is reduced. As such, this species is transferred from *Diacodexis* to *Bunophorus* and includes Sinclair's (1914) hypodigm of *D. robustus* except AMNH 15513 and AMNH 15510, material referred elsewhere (Krishtalka and Stucky, 1986) to *Simpsonodus chacensis.* Although similar in size, *B. robustus* differs from *S. chacensis* in its greater bunodonty, relatively inflated P_4 and lower-crowned molars with shallower talonid basins and less elevated trigonids.

B. robustus also overlaps in size with some specimens of *D. secans* lineage segment *D. s.-secans* (Krishtalka and Stucky, 1985), but is distinguished by a more robust P_4 and more bunodont lower molars that lack postmetacristids and talonid notches and retain relatively large paraconids.

B. robustus, recovered from early Wasatchian deposits in Wyoming and Colorado, is the oldest known and most primitive species of *Bunophorus* in that it is least robust and retains a well-developed paraconid on P_4–M_3. Upper molars (all M^3s) are bunodont, with bulbous cusps and relatively indistinct conule cristae.

Several studies have cited the occurrence of "*D. robustus*" in early Eocene faunas (Gazin, 1962:81; Bown, 1979:108; Schankler, 1980:105; Gingerich, 1985:31; 1989: 58, Fig. 37), but given the lack of adequate morphological descriptions (other than size) and illustrations, assignment of this material is not attempted here.

Bunophorus cappettai Sudre, Russell, Louis and Savage, 1983

Sudre *et al.* (1983) referred specimens from Mutigny, Avenay and Pourcy, France, all of Ypresian age, to a new species of *Bunophorus, B. cappettai.* The holotype (MU 6183) and topotypic material from Mutigny differ in a number of features from North American species of *Bunophorus*: they lack the robusticity typical of that genus; the metaconule on M^2 is enlarged; the paraconid on M_{2-3} is separate from rather than conjoined with the metaconid (not shown in Sudre *et al.,* 1983, fig. 15c); the M_3 hypoconulid lobe is severely reduced; on M_2, the hypoconulid is enlarged on the postcingulid and the trigonid basin is well defined; and the single figured P_4 (Sudre *et al.,* 1983, fig. 15d; specimen not seen) apparently has a small paraconid and prominent metaconid, which is not typical of *Bunophorus.*

The Mutigny specimens (except P_4) resemble *Simpsonodus chacensis* (Krishtalka and Stucky, 1986) in all of these features (except reduction of the M_3 hypoconulid), which suggests that this material pertains to that genus rather than *Bunophorus.*

Two of the specimens referred to *B. cappettai* do appear to represent *Bunophorus*: AV 4666, an M_3 from Avenay; and PY 64-L, an M_3 from Pourcy. The Pourcy specimen resembles material referred above to *Bunophorus robustus* in size, strength of the paraconid, inflation of the talonid cusps and robusticity, but has a cuspule in the talonid basin not found in the latter. The molar from Avenay is similar in size and crown morphology to *B. robustus* and *B. pattersoni.* Neither tooth can be assigned to a known species until more material is recovered from Avenay and Pourcy.

CONCLUSIONS

Study of the type specimens and available collections of *Wasatchia* and *Bunophorus* corroborate Van Valen's (1971) conclusion that these taxa are congeneric. *Bunophorus* has priority and includes six species from the early and middle Eocene of North America: *B. etsagicus* (type species), *B. grangeri* (=*W. lysitensis* and *W. dorseyana*), *B. pattersoni, B. macropternus, B. sinclairi* (=*B. gazini*) and *B. robustus* (=*Diacodexis robustus*). *B. sinclairi* is divided into two subspecies to reflect penecontemporaneous geographic variants: *B. s. sinclairi* from the Wind River, Piceance and Green River basins, and *B. s. robinsoni,* n. ssp., from the Huerfano Basin. Of the specimens identified by Sudre *et al.* (1983) as *Bunophorus cappettai,* the holotype and referred material from Mutigny, France, probably belong to the genus *Simpsonodus,* whereas two molars from Avenay and Pourcy are referable to an undetermined species of *Bunophorus.*

Four of the North American species of *Bunophorus* occur in the Wind River

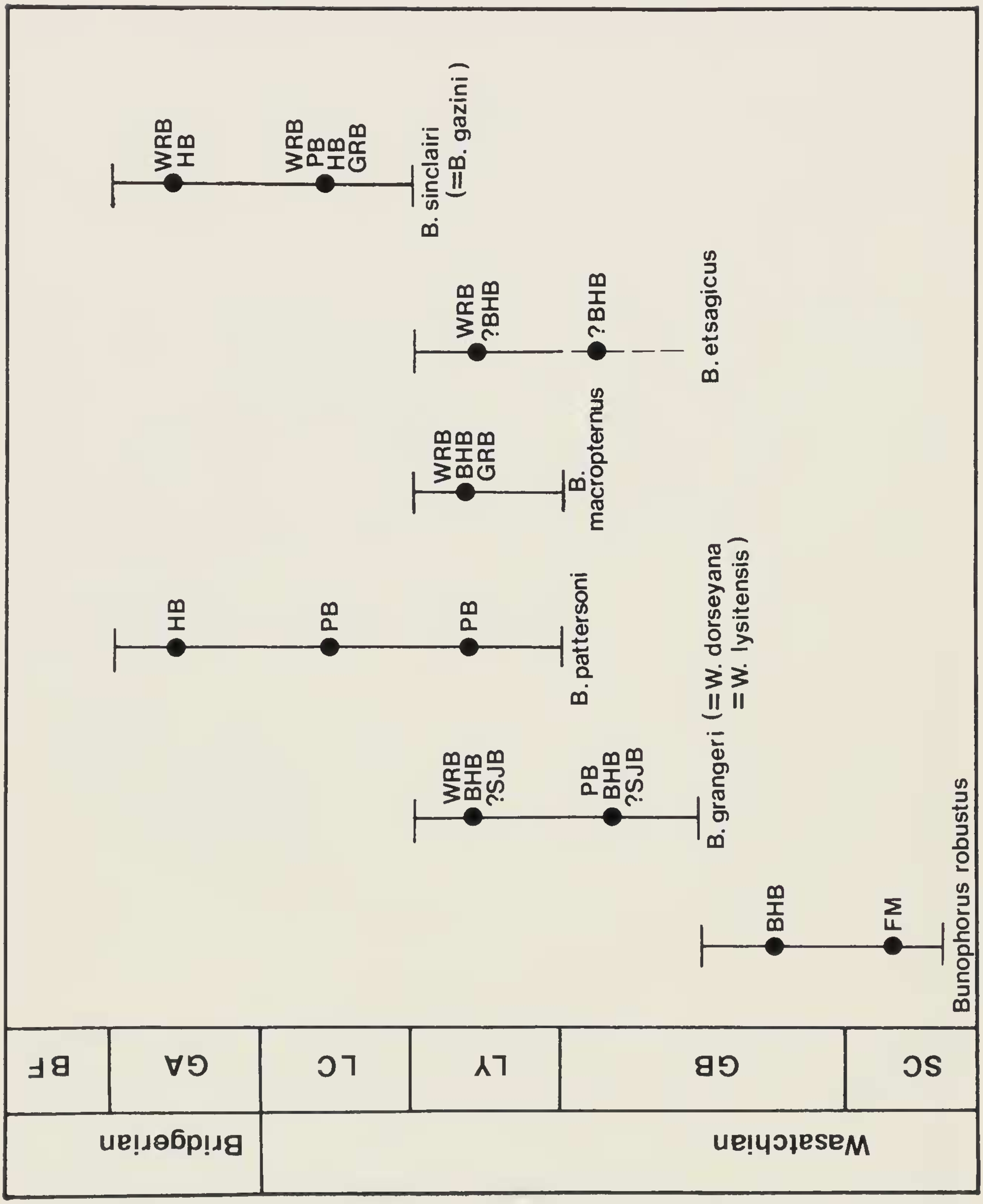
Basin: *B. grangeri, B. macropternus* and *B. etsagicus* in the Lysitean, and *B. sinclairi* in the Lostcabinian and Gardnerbuttean. The widespread co-occurrence of the three Lysitean species is biostratigraphically useful for delineating and correlating sediments of that age; *B. macropternus* alone appears to be a reliable indicator of the Lysitean whereas the occurrence of *B. sinclairi* signifies a late Wasatchian (Lostcabinian) or early Bridgerian (Gardnerbuttean) age. The known records of the North American species of *Bunophorus* are charted in Fig. 7).

The Bunophorinae and Diacodexeinae (*Diacodexis* and *Simpsonodus*; Krishtalka and Stucky., 1985, 1986) together are the most primitive subfamilies of the order Artiodactyla (Fig. 8), node 1, artiodactyl tarsus). *Bunophorus* and the Bunophorinae are a monophyletic group all species of which share the derived features of robust, bunodont cheek teeth (Fig. 8, node 2; see also Krishtalka and Stucky, 1985). *Bunophorus robustus* is the most primitive species in this clade. In *B. grangeri,* the P_4 paraconid is reduced or vestigial (Fig. 8, node 3) and in *B. pattersoni* the molar paraconid is reduced (Fig. 8, node 4). These conditions are further derived in *B. sinclairi, B. etsagicus* and *B. macropternus* in that the paraconid is lost on P_4 and vestigial or absent on the lower molars (Fig. 8, node 5). Within this clade, *B. macropternus* and *B. etsagicus* share inflation of P4/4, with P_4 bulbous anteriorly in proportion to M_1 (Fig. 8, node 6). Beyond these synapomorphies, *B. etsagicus* achieves large size (Fig. 8, node 7) and *B. macropternus* develops hyperinflated P4/4 compared to M_1, lingually hyperinflated upper molars and a strong cingulid on M_3 (Fig. 8, node 8). *Bunophorus sinclairi* exhibits a number of different derived traits including larger size, more bunodont P_4–M_3, a metaconid on P_4, lower molars with a weak or vestigial cristid obliqua and trigonid and talonid subequal in height, and M^{1-2} with hypocone, pericone and isolated metaconule (Fig. 8, node 9).

The polarities of the shared-derived dental features and the implied phylogenetic relationships of these species are consistent with the stratigraphic record. The evolutionary patterns in *Bunophorus,* as revealed by the dentition, contrast markedly with those inferred by us for *Diacodexis* (Krishtalka and Stucky, 1985): the record implies considerable anagenetic change in the frequency and degree of expression of derived morphological features in the species-lineage *D. secans* over seven million years. Species of *Bunophorus,* on the other hand, are short-lived geologically, exhibit relative morphologic stasis through time, and its sister species are marked by discrete breaks in morphology. Some sister species (e.g., *B. robustus* and *B. grangeri*) have the morphology and geologic record that could imply (and, at least, does not falsify) an ancestor-descendant relationship.

Our recognition of two subspecies of *B. sinclairi* is in keeping with our solution to the nomenclatural dilemma of expressing and differentiating temporal variation from geographic variation in a species-lineage in the fossil record (Krishtalka and Stucky, 1985). We designated four "informal lineage segments" to express the stages of anagenetic temporal change in the apparently continuous species-lineage *Diacodexis secans.* In contrast, we advocated that "subspecies" in the fossil record be reserved for expressing spatial patterns (geographic variation) in penecontemporaneous populations of a species. As such, the subspecies of *B. sinclairi* described above highlight the dental differences in this species across approximately 660 km of geographic space in the Lostcabinian and Gardnerbuttean.

Bown and Rose (1987), commendably, also attempted to express significant anagenetic change in their taxonomy of early Eocene anaptomorphid primates. Unfortunately, they seriously misunderstood our approach by mistaking our con-


Wasatchian
Bridgerian
SC
GB
LY
LC
GA
BF
Bunophorus robustus
FM
BHB
B. grangeri (=W. dorseyana =W. lysitensis)
PB BHB ?SJB
WRB BHB ?SJB
B. pattersoni
PB
PB
HB
B. macropternus
WRB BHB GRB
B. etsagicus
?BHB
WRB ?BHB
B. sinclairi (=B. gazini)
WRB PB HB GRB
WRB HB

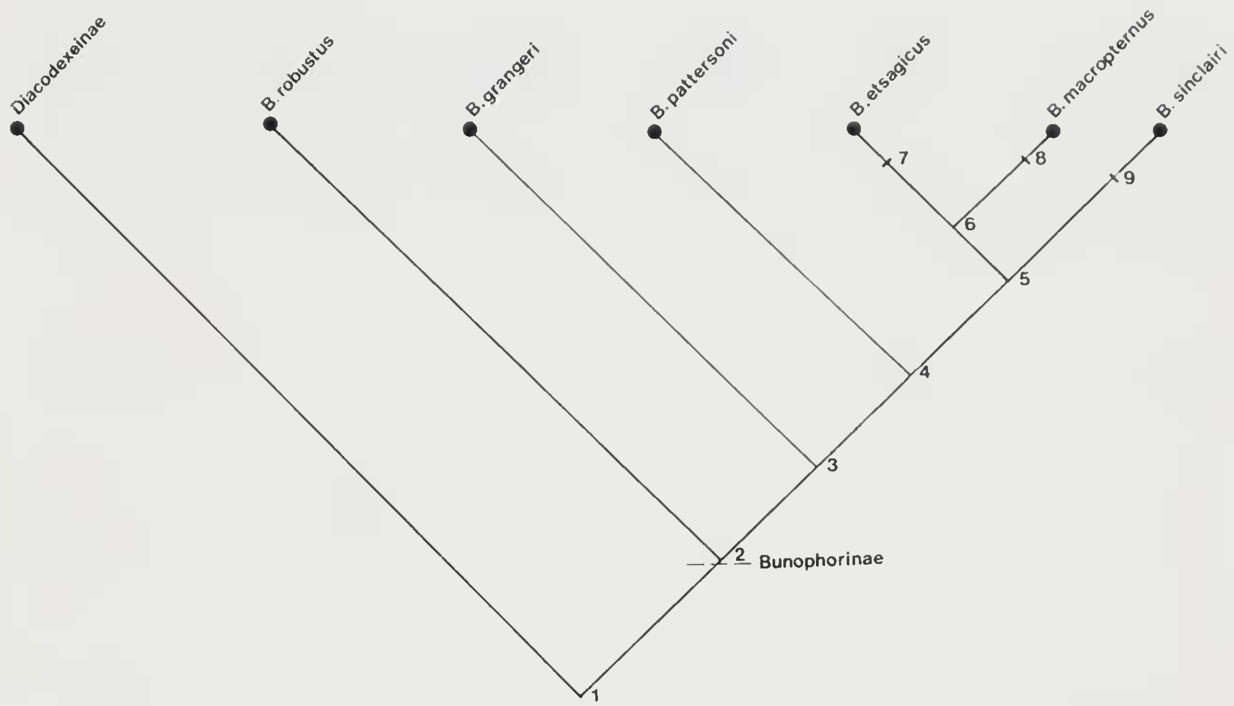


Fig. 8.—Phylogenetic relationships of the species of *Bunophorus*. Node 2: Robust, bunodont P4/4–M3/3. Node 3: P_4 paraconid extremely reduced or vestigial. Node 4: M_{1-3} paraconid reduced. Node 5: P_4 paraconid absent; M_{1-3} paraconid vestigial or absent. Node 6: P^4 inflated and P_4 inflated and bulbous anteriorly in proportion to the molars. Node 7: large size. Node 8: P4/4 hyperinflated in proportion to M1/1; M^{1-3} hyperinflated lingually, M_3 with strong cingulid. Node 9: larger size; P_4-M_3 more bunodont; P_4 with metaconid; M_{1-3} with weak or vestigial cristid obliqua and with talonid and trigonid subequal in height; M^{1-2} with hypocone, pericone and isolated metaconule.

cept and use of "lineage segment" for "formal Linnaean binomina" (Bown and Rose, 1987:24). We (Krishtalka and Stucky, 1985:418) stated clearly that "we divide a species-lineage into *informal* lineage segments, which are temporally successive and morphologically overlapping units." The four lineage-segments of *Diacodexis secans* are informal trinomina with fuzzy morphological boundaries. They are also, we think, a much less cumbersome solution than the hyphenated quadrinomina (e.g., "*Tetonius matthewi-Pseudotetonius ambiqua* intermediates") that Bown and Rose (1987:91) propose for intermediate transitions between paleontological "species." As they say (Bown and Rose, 1987:24), "no scheme would meet with universal acceptance," but a system is needed to express this sort of evolutionary change, whether it employs "stages of evolution" (Maglio, 1971), informal trinomina or another nomenclatural scheme. Such emendation of the Linnaean system to reflect temporal evolutionary patterns is crucial to expressing and recognizing the processes of anagenesis, cladogenesis and geographic variation as they are implied by the fossil record.

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Fig. 7.—Known occurrence (diagrammatic) of the species of *Bunophorus*. Abbreviations: Land Mammal Sub-ages—SC, Sandcouleean; GB, Graybullian; LY, Lysitcan; LC, Lostcabinian; GB, Gardnerbuttean; BF, Blacksforkian. Localities—BHB, Bighorn Basin; FM, Four Mile; GRB, Green River Basin; HB, Huerfano Basin; PB, Piceance Basin; SJB, San Juan Basin; WRB, Wind River Basin.

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